

THE DISTRIBUTION OF MESOZOIC FRESHWATER FISHES

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- Summary.** — 1. Two new terms are introduced to qualify primary division freshwater fish groups: archaicolimnic, originating in fresh waters and always so confined; and telolimnic, confined to fresh waters at present, but less closely restricted in the past. A Recent primary group can only be assigned to the second of these categories on the evidence of marine fossils which are undoubted members of that taxon.
2. Fossil freshwater species can only be assigned to the primary freshwater category on the basis of unequivocal membership of a Recent primary group. Extinct groups of fishes cannot be used as reliable evidence of past continental connections.
3. The only reliably identified Mesozoic primary freshwater fish is the biodontid *Lycoptera*, from near the Jurassic/Cretaceous boundary in N. E. Asia. This occurrence is not consonant with a Gondwana origin of Osteoglossomorpha according to conventional models of late Mesozoic geography, where Asia and Gondwana are separated by Tethys. Evidence is provided that the early Tertiary, marine *Brychaetus* is a true osteoglossoid, implying that the osteoglossoids are a telolimnic group. This, in turn, implies that the Osteoglossomorpha as a whole may have had a marine origin. The highly disjunct distribution of late Mesozoic osteoglossomorphs (according to conventional drift models) supports this hypothesis.
4. Late Mesozoic freshwater fish faunas are sparse and impoverished in comparison with contemporary marine faunas. There is no evidence to warrant the hypothesis that many major teleostean groups arose in Mesozoic fresh waters.
5. Ostariophysan distribution does not seem to be more readily explained by the Gondwana-Laurasia model than by a fixed continent model. While the drift model accounts for characin distribution, it does not explain the abundance of cyprinoids in S. E. Asia coupled with the absence of primary ostariophysans in Madagascar and Australia, or the early appearance of fossil cyprinoids in Europe and North America, of characins in Europe and of silurids in North America.
6. The structure of the Lower Cretaceous chanoid *Tharrhias* indicates that ostariophysans and gonorynchiforms acquired their distinctive cranial skeletons in parallel. Parallel evolution of this sort makes it difficult to suggest characters by which early ostariophysan fossils could be recognised. It is possible that Lower Cretaceous ostariophysans have been found, but not recognised.
7. The life-cycle of *Chanos* suggests a model for the origin of ostariophysans, and implies that they were initially more tolerant of salt water.
8. As a general conclusion, one may say that the Gondwana-Laurasia model is not a great improvement on a fixed continent model in explaining the distribution of freshwater fishes. Characin distribution and the early Cretaceous correlation between the freshwater fish faunas of Brazil and West Africa are explained by late Mesozoic union between South America and Africa, but other aspects of the break-up of Gondwana are not readily correlated with the present distribution of freshwater fishes. Marine origin or influence provides an equally plausible explanation of osteoglossomorph distribution, and may well have played a part in ostariophysan distribution. Progress in understanding the distribution of freshwater fishes is likely to come from analysis of the relationships of such groups as the ostariophysans and the primary freshwater scanthopterygians, rather than from improved paleogeographic models.

INTRODUCTION

In 1922, the distribution of ostariophysan fishes led C. Tate Regan to write 'in early Cretaceous times S. America and Africa formed one continent, which must have extended to India... in late Cretaceous times India appears to have separated from Africa and it probably became connected with Eastern Asia towards the end of the Cretaceous' (Regan 1922, pp. 206-7). Within the last few years, wandering of the continental plates has become an accepted fact through geophysical work, uninfluenced by zoogeographic evidence. Although there are still gaps to be filled, geophysicists seem now to have established the course and timing of the major continental movements since the early Mesozoic. The aim of this paper is to re-examine the distribution of living primary freshwater fishes and their fossil relatives in the light of the new geophysical evidence, to discover whether these distributions are more economically explained by the Gondwana-Laurasia model of late Mesozoic geography than by a fixed continent model. I am grateful to Miss Alison Longbottom, who drew figures 1-5, and to Dr. D. E. Rosen, who commented on a draft manuscript.

METHODOLOGY

Myers (1938, 1949) first pointed out that in analysis of freshwater fish distribution inferences of continental connections or 'land bridges' may only be based upon primary freshwater groups; those which are, so far as we know, 'strictly intolerant of salt sea water' by deep-seated and apparently ancient difficulties of osmotic regulation'. Myers' primary freshwater category obviously carries the implication that the groups involved arose in fresh waters, and have always been so restricted, although usage has been varied. It will be suggested below that two distinct types of group are included within this category. Amongst living fishes, the primary freshwater category includes the lungfishes, *Polypterus*, paddlefishes, *Ania*, and about 6650 species of teleosts, almost exactly one-third of the total number of living teleost species (Cohen 1970). Of these 6650 species, 6200 or 93% are ostariophysans.

Recent freshwater fishes can be assigned to the primary category or to another of the categories defined by Myers on the basis of observation of their distribution and experimental testing of their physiology. Obviously, it is necessary to make similar discriminations amongst fossil fishes if they are to be used in zoogeographic discussions. The only criterion for assigning any fossil species to the primary freshwater category is reliable evidence that it belongs to a group whose living members are, without exception, primary freshwater fishes. If it can be established that a fish-bearing deposit was laid down in fresh waters, without any marine influence (often a difficult enough problem), there is still no reason to assign the contained species to any particular one of the six ecological or physiological freshwater categories defined by Myers. Even if some fossil taxon occurs repeatedly in freshwater deposits, and nowhere else, we are not justified on this evidence in referring it to the primary freshwater category, for catadromous fishes like *Anguilla* which migrate to the sea to breed and secondary freshwater fishes like *Lepisosteus*, which occasionally enter the sea, would give the same picture. A fossil species must be unequivocally assigned to a living primary freshwater group before it can be used in discussions of continental distribution in the past.

Discovery in marine or brackish water deposits of a fossil species belonging to a group whose living members are all primary freshwater fishes will lead one to question whether that group is truly primary, in the sense of having arisen and always remained in fresh waters, or whether the earlier members of the group were less intolerant of salt water, suggesting that the group is an unreliable indicator in zoogeographical arguments. This point can be explored by means of examples in the Percopsiformes and Dipnoi.

The paracanthopterygian order Percopsiformes is represented by three living families, Percopsidae, Aphredoderidae and Amblyopsidae, all primary freshwater fishes of North America. All fossil Percopsidae and Aphredoderidae are from Tertiary freshwater deposits in North America, and no fossil

amblyopsids are known. A single Cretaceous percopsiform genus is known, *Sphenoccephalus*, from marine deposits in Germany (Rosen & Patterson 1969). The relationships of the three extant percopsiform families and *Sphenoccephalus* are shown in figure 1. The position assigned to *Sphenoccephalus* in figure 1 is somewhat arbitrary, for it is possible that this fossil is a primitive percopsid or a primitive

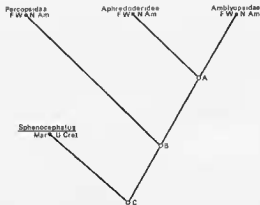


FIG. 1. — Relationships of percopsiform fishes.

aphredodoroid, fitting in somewhere along the line AB. But *Sphenoccephalus* is a very primitive form and exhibits no derived characters to show that it belongs above the point B in the dendrogram. In this case, therefore, the hypothesis that the three living percopsiform families arose in fresh waters (species B) can still be maintained, and further evidence would be necessary to discriminate between the hypotheses that species C was marine, freshwater or diadromous (Nelson 1969a). Such evidence might be provided by the habitat of the sister-group of this assemblage (probably the remaining paracanthopterygians, a predominantly marine group), or by the distribution of the living forms: if, for example, the percopsids occurred in Africa, not North America, the most economical hypothesis would be that species C was marine. Assignment of the marine *Sphenoccephalus* to the Percopsiformes does not destroy the hypothesis that percopsoids and aphredodoroids arose in fresh waters, and does not remove those subgroups from the primary category, but it removes the order Percopsiformes as a whole from this category.

The disjunct distribution of living dipnoans is well known. Fig. 2 shows the relationships of the three living genera and the approximate position of the Lower Triassic *Paraceratodus*, which occurs in marine beds in Madagascar, and of certain Triassic species of *Ceratodus*, also found in marine beds (Lehman 1966, p. 290). Unless it is suggested that the Lepidosirenidae are in fact more closely related to *Neoceratodus* than are *Ceratodus* and *Paraceratodus*, the occurrence of these fossils in marine beds destroys the hypothesis that living dipnoans are a primary freshwater group, originating and always strictly confined to fresh waters, and removes the Ceratodontidae from the primary category. The Lepidosirenidae, however, still appear to be a true primary group, and their present distribution is economically explained by a late Mesozoic connection between Africa and South America.

The term 'primary freshwater group' is customarily used only at the family level and above, since Myers (1949) adopts the category 'vicarious freshwater fishes' for freshwater genera of mainly marine families. It is possible to speak of primary freshwater suborders (Esocoidi, Aphredoderoidi) or orders (Mormyriiformes, Cypriniformes). Such groups, as shown above, are of two types: there are those whose present distribution and physiology, fossil record and relationships all allow one to maintain the hypothesis that the group arose in fresh waters and has always been so restricted; and

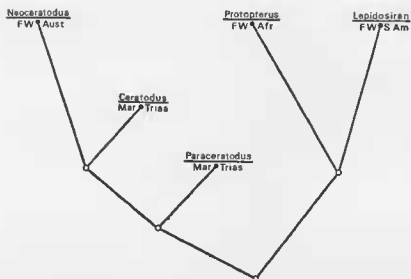


FIG. 2. — Relationships of certain lungfishes

there are those which are included in the primary category because of their present distribution and physiology, but which are shown by their fossil record and relationships to have been less intolerant of salt water in the past, and for which a marine origin can be postulated. For these two types of primary freshwater fishes I propose the names *archaeolimnic* (originating in fresh waters and always so confined) and *telolimnic* (less closely restricted to fresh waters in the past). In no group will it ever be possible to *prove* the original habitat by pinpointing fossil ancestors, so to regard any primary group as archaeolimnic or telolimnic can only be a hypothesis, held with more or less confidence. Of course, all Recent primary groups should be assumed to be archaeolimnic unless there is evidence to the contrary; but these assumptions should be recognised for what they are, and such contrary evidence might be provided only by highly disjunct distribution, inexplicable on our knowledge of past continental wandering. In the case of apparently archaeolimnic groups with an ample fossil record, assessment of the palaeoecology of each fossil-bearing stratum will provide a test of the hypothesis, and some groups (for example esocoids and cyprinoids) pass many such tests. As shown above with the percopsiforms, the discovery of marine fossils within a group does not necessarily destroy the hypothesis that the component subgroups are archaeolimnic, but fossils show that the Percopsiforms as a whole, the Ceratodontidae and Dipnoi are telolimnic. *Amia* also probably belongs to this category.

THE MESOZOIC RECORD

To recapitulate the preceding section, in zoogeographic arguments invoking past continental connections, the only reliable fishes are those assigned to archaeolimnic taxa. No fossil species can be regarded as a primary freshwater fish except on the basis of its assignment to a Recent archaeolimnic group.

In the Mesozoic, such assignments are very rare. There are over 400 living teleostean families, and only 14 (about 3.5%) of these can be recognised with any confidence in the Mesozoic. These families are the Elopidae, Megalopidae, Albulidae, Halosauridae, Clupeidae, Hiodontidae, Aulopidae, Synodontidae, Gonorynchidae, Chanidae, Polymixiidae, Trachichthyidae, Holocentridae and Sciaenidae (Patterson 1967; Rosen & Patterson 1969; Greenwood 1970; Rosen 1973). Amongst these 15 families, only one, the Hiodontidae, is in the primary freshwater category. Undescribed material in Rio de

Janeiro suggests one other possible record of a primary family in the Lower Cretaceous, an osteoglossid from Minas Gerais, Brazil (Santos, personal comm.). At the subordinal level, the proportion represented in the Mesozoic rises to about 15% (15 out of 92 Recent suborders in the classification of Greenwood *et al.* 1966) with the incorporation of marine forms not assignable to family in the Anguilloidei, Alepisauridae, Myctophoidae and Veliferoidei, and at the ordinal level to 45% (14 out of 31 Recent orders) with the addition of forms not assignable to suborder in the Salmoniformes (all marine), Siluriformes (? brackish : Schaeffer 1963; Braniff, Hoffstetter & Signeux 1964; Wenz 1969) and Percopiformes (marine). Only one primary freshwater group, the Hiodontidae, is at present recognisable in the Mesozoic, and there is a possibility that a second osteoglossomorph family, the Osteoglossidae, is also represented. The Osteoglossomorpha will therefore be discussed first, before considering why no other primary group should have Mesozoic representatives.

OSTEOGLOSSOMORPHIA

The osteoglossomorphs are a primary freshwater cohort of primitive teleosts containing six Recent families, Hiodontidae (N. America), Notopteridae (S. E. Asia, Africa), Mormyridae, Gymnarchidae (both Africa), Osteoglossidae (S. America, Africa, S. E. Asia, Australia) and Pantodontidae (monotypic, Africa). Early Tertiary fossils extend the range of the Osteoglossidae into North America, and show that hiodontids, notopterids and osteoglossids were already present within or close to their present range. In the Mesozoic, the Hiodontidae are represented by *Lycoptera* from late Jurassic or early Cretaceous freshwater beds in China, Mongolia and Siberia (Greenwood 1970), and the Osteoglossidae are possibly represented by undescribed material from Lower Cretaceous (? freshwater : Scorza & Santos 1955) beds in Brazil.

Nelson (1969b) attempted a detailed analysis of osteoglossomorph zoogeography, past and present (fig. 3). He found that 'a simple and comprehensive theory regarding past distribution cannot be formulated' because of uncertainty about the phyletic relationships of living forms, especially Hiodontidae, mormyrids and some osteoglossids. Greenwood (1971) has produced new evidence on the relationships of mormyrids, which he coordinates with the notopterids, but the position of Hiodontidae remains uncertain. In any case, moving the mormyrids from the left to the right side of figure 3 would make little difference to the zoogeographic hypotheses involved.

The Mesozoic *Lycoptera*, if it can be accepted as a genuine hiodontid (and not, for example, an early notopteroid or an unassignable member of the hiodontid-notopteroid stock), gives a minimum age for the separation of the osteoglossomorph subgroups, implying the existence at that time of notopteroids and osteoglossids. *Lycoptera* also confirms the past North Asian distribution of hiodontids that Nelson postulated. However, the occurrence of hiodontids in N. E. Asia as early as the lowermost Cretaceous raises severe difficulties for Nelson's hypothesis of osteoglossomorph origins in Gondwana, for at that time the Tethys ocean is thought to have separated Asia from the southern supercontinent (fig. 4). The only possible continental connection between the two seems to be through S. E. Asia (Indo-China, Thailand and the northern part of the Indo-Australian archipelago). Recent work (Ridd 1971) suggests that S. E. Asia once formed part of Gondwana, fitting between India and Australia. It is supposed that, like India, S. E. Asia moved northwards and collided with mainland Asia in the Tertiary, the suture between the two being the Song Ma fault and fold belt. But there is no evidence of an Alpine orogeny along this line, nor of post-Triassic sediments, so that it is possible that the connection between S. E. Asia and mainland Asia is of long standing. But according to conventional models (Jardine & McKenzie 1972; Smith, Briden & Drewry 1973) the only feasible mode of transport of primary freshwater fishes from the southern supercontinent into Asia is as passengers upon the Indian sub-continent or S. E. Asia, which did not arrive in their present position until the Tertiary, long after the *Lycoptera* fauna of N. E. Asia. *Lycoptera*, in fact, seems to suggest only that osteoglossomorph distribution was as disjunct in the early Cretaceous as it is now, and raises problems of faunal distribution analogous to those produced by the presence of the Triassic *Cynognathus* and *Lystrosaurus* tetrapod faunas (otherwise known only from Gondwana) in China (Colbert 1971).

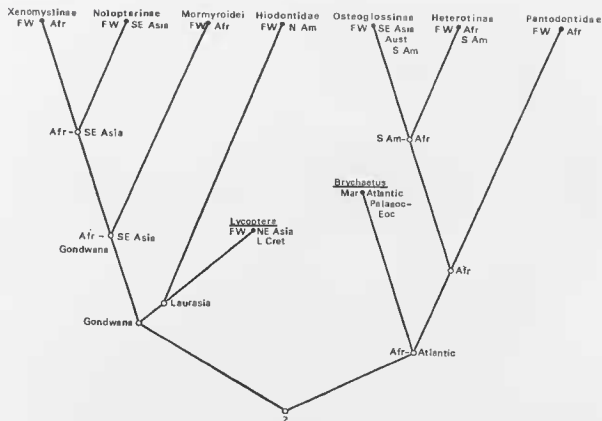


FIG. 3. — Relationships of osteoglossomorph fishes (based on Nelson 1969b)

Although it is not a Mesozoic form, the Palaeocene and Eocene *Brychaetus* deserves mention here. *Brychaetus* occurs in marine beds in Zaïre (Palaeocene, Darteville & Casier 1959; Taverne 1969), Morocco (L. Eocene, Arambourg 1952), S. E. England (L. Eocene, Casier 1966), and there is a closely related form in N. Denmark (L. Eocene, Bonde 1966). Because it is inadequately known, and perhaps because of its apparent marine habitat, ichthyologists (Myers 1938, p. 351; Greenwood *et al.* 1966, p. 364; Nelson 1969b, p. 25) have been unwilling to accept *Brychaetus* as a member of the Osteoglossidae, the family in which it has until now been placed. Taverne (1969) redescribed an osteoglossomorph caudal skeleton from Zaïre and assigned it to *Brychaetus*. This caudal skeleton has a neural spine on the first ural centrum a, diagnostic character of osteoglossomorphs (Greenwood 1967, p. 595). Evidence from the skull of *Brychaetus muelleri* (London Clay) combined with this caudal skeleton evidence is sufficient in my opinion to show that *Brychaetus* is an osteoglossomorph. This evidence may be summarised as follows:

1. The circumorbital series contains only three bones between the lacrymal and dermosphenotic (personal observation; cf. Nelson 1969b, p. 8).
2. The dermosphenotic lies well in front of the autosphenotic, not in contact with the latter.
3. The parapophyses of the abdominal vertebrae are fused to the centra, project transversely, and bear a groove on their postero-dorsal surfaces ending in a deep pit which received the head of the pleural rib (personal observation).
4. In the caudal skeleton, there is a neural spine on U1 and the upper hypurals fuse with U2.

Within the Osteoglossomorpha, the characters which have previously been used to relate *Brychaetus* to the Osteoglossidae are indecisive. Nevertheless, there are a few trenchant features indicative of osteoglossoid relationships:

1. There is a basiptyergoid process on the parasphenoid, articulating with the endopterygoid and overlapped dorsally by a long antero-ventral process of the hyomandibular (Roellig 1967 and personal observations). Although a basiptyergoid process is a primitive feature, in primitive actinopterygians it articulates with the metapterygoid, and the arrangement just described is unique to osteoglossoids and *Brychaetus*.
2. There is no discernible suture between the palatine and ectopterygoid (cf. Ridewood 1905).
3. There is a large, expanded tooth-plate in the floor of the mouth which covers the first ossified basi-branchial (first or second) and extends forwards above the anterior ends of the ceratohyals (cf. Nelson 1968).

These characters, in conjunction with the osteoglossoid-like jaws, infraorbitals, operculum, etc., seem to be sufficient to justify placing *Brychaetus* in the Osteoglossoidi. It is not possible to show that *Brychaetus* is more closely related to *Pantodon* than to the Osteoglossidae, nor that it is closer to one osteoglossid subfamily than the other. The position assigned to *Brychaetus* in figure 3 agrees with what is so far known of its anatomy. It has been argued that the marine beds in which *Brychaetus* is found are not evidence of its true habitat, but that the individuals preserved had floated out from their original fluviatile habitat as corpses (Roellig 1967). While such an explanation might account for one or two fragmentary specimens, I do not believe it is consonant with the number of well preserved individuals of *Brychaetus* found in the London Clay, and I agree with Gosic (1966, p. 144) that the wide distribution of the genus is strong evidence against such an interpretation.

In the Palaeocene and Eocene, therefore, there was a well attested marine osteoglossoid distributed over about 50° of latitude in what is now the western Atlantic. The addition of *Brychaetus* to Nelson's outline of osteoglossomorph historical geography (fig. 3) alters the picture considerably, for it adds a new hypothesis for the place of origin of the osteoglossoids, suggesting that they may be a telimnic group, and that they may have achieved their cosmopolitan distribution by means of seaways. This, in turn, offers a further hypothesis for the place of origin of the Osteoglossomorpha as a whole. As has been pointed out above, assignment of *Lycoptera* to the Hiodontidae (or Notopteroidei) raises severe difficulties for a Gondwana origin of the Osteoglossomorpha. Only if there has been a long-standing connection, through S. E. Asia, between Laurasia and Gondwana, can a primary late Mesozoic distribution in both supercontinents be explained; if the conventional view of the history of Gondwana is accepted, a marine origin of the Osteoglossomorpha is indicated.

MESOZOIC FRESHWATER FAUNAS

The Osteoglossomorpha, just discussed, are the only primary freshwater teleostean group represented by fossils in the Mesozoic. Why should other primary groups not have been found? Greenwood *et al.* (1966), Myers (1967) and others have suggested that some of these groups, notably amongst the Ostariophysii, must have been in existence then. Myers discusses this question with special reference to ostariophysians. 'That we have found no Mesozoic fossil characoids or other cypriniform ostariophysians is not surprising. Unlike marine deposits, fluviatile and lake deposits are rarely of wide geographical extent and are highly subject to quick subsequent erosion by the same streams which laid them down ...' the center of origin of these fishes [ostariophysians] — in a Mesozoic southern continent — is in an area where there has been comparatively little search for freshwater fish-bearing deposits' (Myers 1967, p. 617). Greenwood *et al.* extend these arguments, writing 'the dearth of Early Mesozoic fossils of teleostean type, except in marine Triassic and Jurassic beds in the area of the Tethys Sea, may be related to a fresh-water origin of many teleostean lines in regions where fresh-water, fish-bearing deposits are rare or undiscovered... the absence in known Cretaceous deposits of several important lines of teleostean development (notably the salmonoids and ostariophysians...) again leads to the suspicion that much teleostean evolution was going on in Mesozoic fresh waters' (1966, p. 347). One may summarise the ideas just quoted in two hypotheses:

- (i) No Mesozoic representatives of such groups as the ostariophysan suborders and the extant salmoniform suborders have been found because the early evolution of these groups occurred in fresh waters, and most late Mesozoic deposits are marine.
- (ii) Those late Mesozoic freshwater deposits which have yielded fishes contain no ostariophysans or salmoniforms because these groups were living elsewhere, in upland waters or other geographic regions.

The inadequacy of the freshwater fossil record is too well known to need re-emphasis. It is sufficiently exemplified by the lack of fossil gymnotoids in South America, of pre-Pliocene characins in Africa, and so on. So far as the salmoniform suborders are concerned, however, absence of these in Cretaceous marine deposits can hardly be regarded as an indication that these groups were then confined to fresh water, for oceanic groups like the alepocephaloids and argentinoids are also unknown in the Cretaceous, and it is impossible to regard these as having originated in fresh water. In any case, however inadequate the fossil record may be, we are obliged to make the most of it.

Figure 4 shows the distribution of the better known late Mesozoic freshwater fish faunas. These are possibly all from coastal plain deposits, as are the North American ones (Estes 1971, p. 155), but



FIG. 4. — Map of Cretaceous geography (as reconstructed by Smith, Briden & Drewry 1973) showing the distribution of the better known late Mesozoic freshwater fish faunas. Key : 1, Hell Creek Formation, U. Cretaceous ; 2, Lance Formation, U. Cretaceous ; 3, Trinity Formation, L. Cretaceous ; 4, Santana Formation, L. Cretaceous ; 5, Brazilian 'Wealden', L. Cretaceous ; 6, Purbeck, U. Jurassic ; 7, European Wealden, L. Cretaceous ; 8, Karatau, U. Jurassic ; 9, *Lycoptera* fauna, U. Jurassic — L. Cretaceous ; 10, West African 'Wealden', L. Cretaceous ; 11, Stanleyville, U. Jurassic ; 12, Talbragar, Jurassic ; 13, Koonwarra, L. Cretaceous.

there is a fair geographic spread (cf. hypothesis (ii) above). There is one generalisation that I think can be applied to all these faunas: in comparison with contemporary marine faunas they are archaic and impoverished. This has been noted independently by many who have worked on individual faunas (Woodward 1919, p. 144; Saint-Seine 1955, p. 114; Yakovlev 1962, p. 97; Estes 1971, pp. 144, 158; Waldman 1971, p. 61). Detailed comparisons to demonstrate this are difficult to make because of problems of stratigraphical and climatic correlation, and also because any environment in which intact fishes are fossilised must be regarded as abnormal. In the late Jurassic (Kimmeridgian), a genuine comparison might be expected from the freshwater fauna of the Stanleyville beds (Zaire) and the underlying marine fauna of the same region (Saint-Seine 1955; Saint-Seine & Casier 1962), but this marine fauna is itself impoverished, perhaps because of bathymetric conditions (Saint-Seine & Casier 1962, p. 1). One interesting comparison between these two African faunas can be made; in the freshwater beds there are no leptocephals or more advanced forms, and about 90% of the individuals preserved are holosteans (*Catavariolus*), while in the (older) marine beds 80% of the individuals are a primitive teleost (*Paracalpusus*), probably a leptocephal (Patterson 1970, p. 287).

In the Lower Cretaceous, comparisons are difficult because of the lack of a well known marine fauna contemporary with the widespread 'Wealden' fauna, and because of the probability of brackish or marine elements in some Wealden faunas. But as a whole, the Wealden fauna seems to be little more than an impoverished version of the late Jurassic marine fauna, with few, very primitive teleosts, the last surviving palaeoniscoids (*Coccolepis*), many holosteans (amioids, pycnodonts, *Lepidotes*) and the last pholidophoroids. The only notable innovations are the earliest herrings (*Diplomystus*) and gonorynchiforms (Chantidae), both also found in early Cretaceous marine beds.

In the Upper Cretaceous, the best known freshwater faunas are those of North America (Estes 1964, 1971; Estes & Berberian 1970), based mainly on fragments and dissociated bones, and perhaps biased for this reason. In comparison with contemporary and older marine faunas from the same region (Niobrara Chalk, Kansas; Mooreville Chalk, Alabama; Applegate 1970), this freshwater fauna is notably archaic and impoverished, containing the last hybodont sharks, the last aspidorhynchids, dominated by holosteans (especially *Amia* and *Lepisosteus*), and with a very limited teleostean fauna. The only innovation is *Platacodon*, referred to the Sciaenidae, a chiefly marine acanthopterygian family of which this is the earliest record.

Such comparisons can be extended into the Lower Tertiary. The early Eocene Green River fauna is perhaps the best known of all fossil freshwater fish faunas, and is contemporary with some well known but geographically distant European faunas (Bolca, Italy; London Clay, Bracklesham and Barton Beds, England). The climate of the Green River lake was probably continental, with winters which may have been comparatively severe, but the mean annual temperature is estimated to have been about 18°C, and therefore broadly comparable with the subtropical climate deduced for the European marine localities. In comparison with the fishes of these marine beds, the Green River fauna is again archaic and impoverished. It contains paddlefishes, *Lepisosteus*, *Amia*, and is dominated by 'double-armoured herrings' (*Diplomystus*, *Knightsia*) which are abundant in marine and freshwater beds throughout the Cretaceous. There are also gonorynchids, a group which is marine in the Cretaceous and today, but contains one freshwater genus found in the Green River lakes and in the Eocene and Oligocene of Europe (Perkins 1970); *Phareodus*, an osteoglossoid; ictalurid catfishes, the earliest members of this endemic North American family; Percopsiformes (two genera of percopsids, and possibly also the problematic *Asineops*: Rosen & Patterson 1969), another group with marine Cretaceous representatives; and two acanthopterygian families, the Serranidae (*Priscacara*, *Cockerellites*), a dominantly marine family, and the Percidae (*Mioplosus*, differs from all living Percidae in having many fewer vertebrae, cf. Collette 1963), a north temperate primary group also known from the Eocene of Europe.

In summary, the evidence of the known late Mesozoic and early Tertiary freshwater fish faunas certainly does not support Myers' contention (1967, p. 617) that 'the Mesozoic origin of many teleostean groups occurred in fresh waters', and hypothesis (i) (p. 163 above) fails this test. Late Mesozoic freshwater faunas of the same archaic and impoverished type are known in Europe, Asia, Africa, South America and Australia. There is, of course, no evidence bearing on hypothesis (ii), for this cannot be tested.

Such evidence as there is indicates that late Mesozoic fresh waters, on every continent, were not centres of evolutionary novelty, but were the last refuge of relict groups — hybodont sharks, palaeo-niscoids, holosteans, aspidurhynchoids, pholidophoroids — formerly widespread in the sea.

OSTARIOPHYSANS

The conclusion reached in the preceding paragraph, that the late Mesozoic fresh waters of which we have evidence were evolutionary backwaters so far as fishes are concerned, will serve as an introduction to the problem of ostariophysan origin and distribution, which has always been the mainstay of ichthyological arguments on past continental connections (Regan 1922, Gosline 1944, Schaeffer 1947, 1952, Myers 1967, Gery 1969). It is not my intention to retreat the ground covered in these papers. The basic facts seem still to be as set out by Regan in 1922 :

- (i) The most primitive ostariophysan group, the characoids, are found only in Africa and in tropical America, a distribution which can be explained by the origin of this group in West Gondwana, before the final separation of the African and South American portions, in or before early Cretaceous times. Primitive characoids are now found on both continents (Roberts 1969), and there is no evidence to suggest that either is the primary site of origin. The discovery of characin teeth in the Eocene of Europe (Cappetta, Russell & Brailon, 1972) adds a third possible site of origin. Recent evidence (McZalira & Paula Couto 1971) suggests that the Tremembé Formation, Sao Paulo, Brazil, which yields the best known fossil characins and is usually considered to be Pleistocene, is Oligocene in age.
- (ii) The siluroids are now cosmopolitan but the primary freshwater families are absent in Australia and Madagascar. The centre of abundance of siluroids is South America, and this is also the home of the primitive *Diplomysetes*. There are no families common to the African and South American primary siluroid faunas, but Africa shares three families with India and south-east Asia. The only new piece of evidence here is the recent discovery of undetermined siluroids in the Upper Cretaceous of Bolivia (Wenz 1969). Siluroid relationships are still too poorly understood for a phyletic analysis, and no proper hypothesis about the place of origin can be set up until such an analysis is made. Siluroid distribution is certainly Gondwanian, and their origin, like that of characins, is likely to have predated the separation of Africa and South America. Similarity between the African and Asian siluroid faunas may only reflect the proximity of these areas during the Tertiary, since India and Africa separated earlier than Africa and South America. The absence of primary siluroids in Madagascar is an important point opposing widespread distribution of siluroids in West Gondwana before break-up.
- (iii) The cyprinoids are absent in South America but show a centre of abundance in south-east Asia, and this has been taken to indicate that they originated there (Regan 1922, Greenwood *et al.* 1966, Myers 1967, etc.). But Gery (1969, p. 35) has pointed out that if the Ostariophysi is a monophyletic group, it must have had a single place of origin which he suggests was Africa, citing the presence of the primitive *Barilius* and related forms in Africa as evidence that this was the original home of cyprinoids. Gery proposes that cyprinoids originated later than characins and siluroids, after the separation of Africa and South America, and spread into Eurasia by land connections not directly involved in the dispersal of fragments of Gondwana. The earliest fossil cyprinoids are found in the basal Eocene of Europe. As in the siluroids, cyprinoid interrelationships are too poorly understood for any sort of analysis, and Greenwood *et al.* (1966, p. 385) have questioned the position of *Barilius* as the most primitive cyprinoid.

Attempts to correlate the supposed history of the ostariophysans with the known history of Gondwana are therefore unsatisfactory, mainly because of lack of knowledge of the interrelationships of living forms. The absence of primary freshwater ostariophysans in Australia and Madagascar opposes widespread distribution of the group in Gondwana: temperature controlled distribution might account for the lack of Australian ostariophysans, but not for Madagascan ones.

Within the Characoidae, Cyprinoidei and Siluriformes phyletic relationships are too poorly understood to erect sound hypotheses about the place of origin of each group. At a higher level, conventional ostariophysan classification implies that characoids and cyprinoids (order Cypriniformes) are more closely related to each other than either is to catfishes (order Siluriformes), but this classification is not phyletic, characoids and cyprinoids being placed together apparently only because both lack the conspicuous specialisations of siluriforms. Known fossils have no direct relevance to the problem of ostariophysan interrelationships. The only freshwater ostariophysan fossils known to occur outside the present range of their group are the new characin teeth from the Eocene of France. Fossils give a minimum age of Upper Cretaceous (? Senonian) for the siluriforms, and show that extension of primary siluriforms into North America and of cyprinoids into North America and Europe had already taken place by the Eocene.

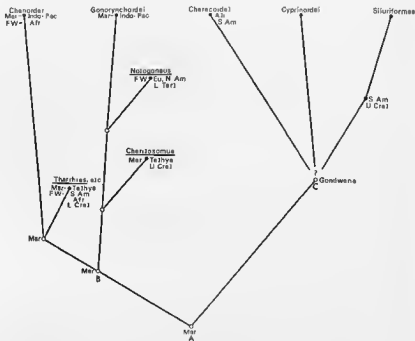


FIG. 5. — Relationships of ostariophysan fishes (sensu Rosen & Greenwood 1970).

Whereas the interrelationships of the main ostariophysan groups remain unknown, recent work suggests that the sister-group of the ostariophysans is the order Gonorynchiiformes (Rosen & Greenwood 1970: these authors include the gonorynchiiforms within the superorder Ostariophysae as a series Anotopsae, but for greater clarity and economy the term Ostariophysae is used here in the conventional sense without including the gonorynchiiforms). The gonorynchiiforms are a small group containing two suborders, Chanoidae (five freshwater genera in Africa and the euryhaline *Chanos*, Indo-Pacific) and Gonorynchoidei (*Gonorynchus* only, Indo-Pacific, marine). The freshwater gonorynchiiform families are unknown as fossils, but the Chanidae and Gonorynchidae have long fossil records. Fossil chanids are known in the Lower Cretaceous of West Africa (*Chanopsis* Casier 1961,

'Wealden', non-marine; *Parachanos* Arambourg & Schneegans 1935, 'Wealden', non-marine), Brazil (*Tharrhias*, *Dastilbe*, Santos & Valença 1968, ? Aptian, non-marine) and Italy (*Chanos leopoldi*, D'Erasmus 1915, ? Albian, marine) and the Upper Cretaceous of Yugoslavia (*Prochanos* Bassani, Cenomanian, marine). Gonorynchids are known from the Upper Cretaceous of Lebanon and Germany (*Charitosomus*, Cenomanian-Campanian, marine) and from the Eocene and Oligocene of Europe and North America (*Notogoneus*, freshwater). Both chanoids and gonorynchoids are therefore shown by fossils to have had a greater geographical range in the past, and the gonorynchids are also shown to have extended into fresh waters.

If chanoids existed in the Lower Cretaceous, then ostariophysans must also have been in existence then, if the relationships shown in figure 5 are correct. Study of one of these Lower Cretaceous chanoids suggests a hypothesis which might account for the apparent absence of ostariophysans in Lower Cretaceous rocks: that they are present, but unrecognisable. Figures 6 and 7 show the skull and caudal

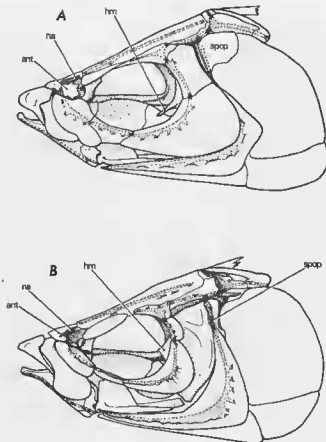


FIG. 6. — A, skull of *Chanos chanos*, Recent, after Ridewood (1904). B, restoration of skull of *Tharrhias araripis* Jordan & Brauner, L. Cretaceous, Santana Formation, Brazil. *ant*, antorbital; *hm*, anterior process of hyomandibular; *na*, nasal; *sppc*, suprapreopercular.

skeleton of the Recent *Chanos* and the Lower Cretaceous *Tharrhias araripis*, from the Santana Formation of Brazil. The skulls of these two fishes are almost identical, and features such as a suprapreopercular, four infraorbitals, highly specialised jaws and complete absence of teeth leave no doubt that they are closely related. But in the caudal skeleton, *Tharrhias* lacks the specialisations which relate the caudal skeleton of *Chanos*, itself the most primitive amongst Recent gonorynchiforms, to those of gonorynchiforms and ostariophysans (fusion of first pre-ural centrum and its neural arch with the ural centra and first uroneural, reduction of head of first hypural). The caudal skeleton of *Thar-*

rhias, with three autogenous uroneurals, the first extending to the second pre-ural centrum, and two free ural centra, is one of the most primitive known amongst euteleosteans (cf. Patterson 1970), and the only features it shows which might relate it to the gonorynchiform-ostariophysan assemblage are the presence of only two epurals and a slight reduction of the head of the first hypural. Chanoids are readily recognisable as fossils because of the the unique specialisations of the skull, notably the complete loss of teeth and the form of the premaxilla. *Tharrhias* shows that these specialisations had appeared while the caudal skeleton was still extremely primitive, and that the distinctive caudal specialisations of chanoids, gonorynchoids and ostariophysans were acquired in parallel. If one constructs a morphotype of the gonorynchiforms (species B, fig. 5), with a caudal skeleton like that of *Tharrhias* and a skull sharing the primitive features of chanoids and gonorynchoids, one might expect

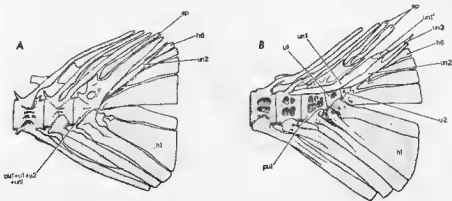


FIG. 7. — A, caudal skeleton of *Chanos chanos*, Recent. B, caudal skeleton of *Tharrhias araripis* Jordau & Danner, L. Cretaceous, Santana Formation, Brazil, from BMNH P. 54331. *ep*, epural; *hb*, hypural; *pa*, preural centrum; *u*, ural centrum; *un*, urogonurium.

to recognise it only by a small, toothless mouth, a common feature of late Jurassic and early Cretaceous teleosts. Species A, the morphotype of gonorynchiforms and ostariophysans, would have a primitive caudal skeleton, a well developed dentition, and would lack the Weberian apparatus. Early ostariophysans (A-C, fig. 5) should be recognisable by the Weberian apparatus, but this would only be visible in exceptionally well preserved fossils. Those familiar with fossil teleosts know that the anterior vertebrae are normally crushed and obscured by the operculum and shoulder girdle, and are very difficult to count, let alone examine in detail. In the Lower Cretaceous there are many small, nondescript teleosts, usually classified as *Leptolepis* or *Cluparus* (see Patterson 1970 for review). Some of these could be early ostariophysans, not recognisable because of lack of distinctive specialisations.

The gonorynchiforms, as the sister-group of the ostariophysans, suggest some speculations on the place and mode of origin of the letter. The life history of *Chanos*, morphologically the most primitive gonorynchiform, seems to me to be of great interest in this connection. Adult *Chanos* are marine, coastal fishes. They breed in inshore waters, producing many pelagic eggs. At a length of about 15 mm, the larvae move inshore and enter brackish pools and creeks, often only connected with open water at extreme high tide, returning to the sea as young adults. In the Far East, *Chanos* is extensively farmed in 'marine fish-ponds' because of this habit, and Sunier (1923) gives a full account of these habitats, noting the extraordinary salinity tolerance of the fishes. The interest of this life history is that the same behaviour is shown by the most primitive living teleosts, *Elops*, *Megalops*, *Tarpon* and *Albula* (Wade 1962). In these elopiform fishes there is a leptocephalus larva, and it is the newly metamorphosed post-larva which moves inshore. The occurrence of this type of life cycle, with an

apparently obligatory post-larval period of development in enclosed creeks or lagoons of highly variable salinity, in the most primitive living teleosts (elopiforms) and the most primitive member of the gonorynchiform-ostariophysan assemblage (*Chanos*) suggests that this may be a primitive teleostean (or even actinopterygian) feature. This hypothesis provides a powerful model for interpreting the variations in habitat and life history found amongst teleosts (and other actinopterygians). Amongst elopomorph fishes, suppression of the 'fish-pond' stage would lead to a life-cycle like that of the deep-water albulid *Pterothrissus*, which migrates into shallower water to breed on the edge of the continental shelf (Poll 1953), and from this to fully oceanic groups like the halosaurs, notacanthids and many eels. Emphasis on the 'fish-pond' stage would lead, on the other hand, to a life-cycle like that of *Anguilla*. Acquisition of sexual maturity during the 'fish-pond' stage is the modification of the elopoid-ghanid life-cycle necessary for fully freshwater life.

Modifications of the elopoid-ghanid type of life-cycle could account for the breeding migrations of diadromous fishes like sturgeons, many clupeoids, salmonids, osmerids and galaxioids, and the euryhalinity of these and other primitive actinopterygians. Fossil evidence bearing on the hypothesis that actinopterygians were primitively euryhaline is naturally sparse. Most early actinopterygian (and teleostome) groups are found in both marine and freshwater deposits, but because of the 'coarseness' of the morphological evidence available in fossils it is hard to find reliable evidence of a single species in both these environments, implying euryhalinity. The only good example known to me is the recent discovery (Cressey & Patterson 1973) of fossil parasitic copepods belonging to an exclusively marine group (Dichelesthioidea) in the gill-chamber of *Cladocyclus* (Ichthyodectidae) from the Lower Cretaceous Santana Formation of Brazil, which is freshwater according to the evidence of ostracods (Bate 1972). This implies that these examples of *Cladocyclus* had recently migrated from the sea, like fresh-run salmon which are recognised by the presence of marine ectoparasites.

With reference to ostariophysans, the hypothesis that teleosts were primitively euryhaline, and that the life-cycle of *Chanos* is primitive, would imply that species A (fig. 5) was an inshore fish of warm seas, whose life-cycle involved an inland phase, in fresh or brackish water. *Gonorynchus* would then be a fish which had dropped this 'fish-pond' stage, while the remaining gonorynchiforms (including the fossil gonorynchid *Notogoneus*) and the ostariophysans would have come to reach sexual maturity in fresh waters and so dropped the marine stage. Such acquisition of sexual maturity implies some initial neoteny, and it seems significant that the African freshwater gonorynchids, especially *Cromeria*, give every indication of neoteny.

Lower Cretaceous chanoids are found in Tethys and on both shores of the central Atlantic, but freshwater chanoids are found only in Africa. This suggests that Africa was the site of origin of the ostariophysans, corroborating Gery's (1969) conclusion based on analysis of living ostariophysans. As to the time of origin of ostariophysans, an upper limit is provided by the first occurrence of undoubted chanoids (Neocomian), a lower limit by the separation from Africa of India and Madagascar, since they lack characins. The latter events are not yet precisely dated, but are unlikely to have been much before the Neocomian. This implies that ostariophysans originated at about the Cretaceous/Jurassic boundary, and were probably initially more tolerant of salinity variations.

A TRANSATLANTIC CRETACEOUS CORRELATION

The remarkable correlation between the non-marine ostracod faunas of the 'Wealden' of north-east Brazil (Bahia Supergroup) and West Africa (Cocobeach Series) (Grekoff & Krümmelbein 1967) has entered the literature as one of the best pieces of zoological evidence for the late Mesozoic continuity of Africa and South America. The fish fauna of these African and Brazilian deposits provides similar evidence, as shown in the table below.

Cocobeach Series of Gabon and Equatorial Guinea (Casier & Taverne 1971)	Ilhas Formation, Brazil (Schaeffer 1947 with later additions)
Coelacanthiformes ¹	<i>Mawsonia gigas</i> Woodward <i>M. minor</i> Woodward
Actinopterygii	
Holostei	
family Semionotidae	
<i>Lepidotes</i> sp. ²	<i>Lepidotes mawsoni</i> Woodward <i>L. souzoi</i> Woodward <i>L. roxoi</i> Santos
family Amiidae	
<i>Urocles</i> sp.	<i>Urocles mawsoni</i> (Woodward)
family Aspidorhynchidae	
<i>Belonostomus</i> sp.	<i>Belonostomus carinatus</i> Woodward
Teleostei	
family ³ Leptolepididae ⁴ (including Clupavidae) ⁵	
<i>Leptolepis congolensis</i> Arambourg & Schlegel	<i>Leptolepis bahiensis</i> Schaeffer <i>Scombroclupeoides scutata</i> (Woodward)
<i>Clupaeus</i> spp.	
family Ichthyodectidae	
<i>Chirocentrus</i> ? <i>guinensis</i> Weiler	<i>Cladocyclus mawsoni</i> (Cope)
two undescribed ichthyodectids	
family Diplomyzidae	
<i>Diplomyzatus goodi</i> Estman	<i>C. woodwardi</i> (Santos)
family Chanidae	
<i>Parachanos aethiopicus</i> (Weiler)	(5)

This comparison between the fishes of the West African and Brazilian Wealden lacks the precision of Grekoff & Krömmelbein's correlation based on ostracods. This is because of lack of stratigraphic details on the provenance of most of the fishes, because both faunas are in need of modern revision, and because comparisons at the species level are made more difficult by incomplete preservation of the fossils. Nevertheless, the resemblance between the two faunas is very remarkable: it is at least as close as that between the Wealden faunas of South-east England (Woodward 1916-1919) and Belgium (Traquair 1914).

1. Although coelacanthids are apparently absent in the Cocobeach Series, *Mawsonia ubangiana* Casier (1961) occurs in the Bokungo Series, Zaire, which is slightly younger but of similar facies.

2. Arambourg & Schlegel (1935, p. 22) remark on the close similarity of the African *Lepidotes* scales to those of the Brazilian *L. mawsoni*.

3. Cretaceous *Leptolepis* and *Clupaeus* species are small, nondescript teleosts of unknown and probably varied relationships. Patterson (1970, p. 289) remarks of *L. bahiensis* and *S. scutata* that either or both could well be close to or synonymous with *L. congolensis*.

4. Schaeffer (1947, fig. 5) places *D. goodi* as the closest relative of *D. longicostatus* and remarks on the very close resemblance between them.

5. No chanids have yet been recorded from the Ilhas Formation, but in the overlying Alagoas Formation (? Aptian) of Rio de Janeiro *Dastibis crandalli* Jordan occurs, and Santos (1947) writes of the 'extraordinary similarity' between *Dastibis* and *Parachanos* and is inclined to consider the latter a synonym of the former.

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ADDENDUM

Since the manuscript of this paper was submitted (July 1972) there has been new work bearing on some of the topics discussed.

Methodology. D. E. Rosen (1974, *Bull. Am. Mus. nat. Hist.*, in the press) has criticised Myers' distinction between primary and secondary freshwater fishes, because records of salt tolerance in supposedly primary fishes are numerous, and because secondary groups such as cichlids and atheriniforms have distributions similar to those of primary groups like ostariophysans, implying that the dispersal of both types is controlled by the same factors. For zoogeographic analyses, Rosen proposes that fishes should be regarded as continental (including primary and secondary freshwater) or oceanic, and that fishes should be assigned to these categories "not by what we imagine to be their habits and possible dispersal mechanisms but by their distribution in relation to phylogeny". These conclusions do not seem to invalidate the concept of archaicolimnic and telolimnic groups proposed in this paper: secondary freshwater fishes could also be assigned to one or other of these categories.

Osteoglossomorpha. G. Nelson (1973, *Am. Mus. Novit.*, 2524) has commented on my conclusions concerning *Brychoetus*, having seen a preprint of this paper. Nelson points out that if *Brychoetus* is the only marine osteoglossomorph known, parsimony demands that we regard it as secondarily marine. He writes "in order to justify any other conclusion, additional forms, related most closely to osteoglossomorphs other than *Brychoetus*, would have to be discovered, and their significance for marine origins determined by a comparative procedure". Other probable marine osteoglossomorphs are *Platinx*, from the Palaeocene of Turkmenia and the Eocene of Italy (P. L. Forey, Ph. D. thesis, London Univ., 1971), and *Opaithrissops* from the Palaeocene of Turkmenia, but neither genus is sufficiently well known for an analysis of relationships.

Ostariophysans. The record of Eocene characoids from Europe is extended to England by the discovery of a single tooth (BMNH P. 56522) from the Blackheath Beds (lowermost Eocene), Abbey Wood, Kent, resembling the *Alestes*-like teeth illustrated by Cappatta, Russell & Brailon (1972). Frizzell & Koenig (*Copeia*, 1973, pp. 692-698) have confirmed that *Vorhisia*, known by otoliths from marine and brackish horizons in the Maastrichtian of South Dakota, is a siluriform, not assignable to family. T. R. Roberts (1973, pp. 373-395 in *Interrelationships of Fishes*, ed. P. H. Greenwood, R. S. Miles & C. Patterson, Academic Press, London) has discussed the interrelationships of Recent ostariophysans, and has produced a new classification of the group in which cyprinoids and characoids are no longer co-ordinated in opposition to siluroids.